Effects of experimental warming and increased precipitation on soil respiration in an alpine meadow in the Northern Tibetan Plateau

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HIGHLIGHTS

- Warming and increased precipitation did not significantly alter soil respiration (R_s).
- Response of R_s to warming showed a quadratic relationship with warming magnitude.
- R_s showed a quadratic relationship with precipitation.

GRAPHICAL ABSTRACT
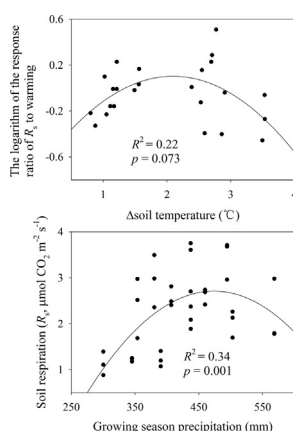
ABSTRACT

Uncertainty on the response of soil respiration (R_s) to warming and increased precipitation on the Tibetan Plateau can limit our ability to predict how alpine ecosystems will respond to future climate change. Based on a warming (control, low- and high-level) and increased precipitation (control, low- and high-level) experiment, the response of R_s to experimental warming and increased precipitation was examined in an alpine meadow in the Northern Tibetan Plateau from 2014 to 2017. The low-level warming increased soil temperature (T_s) by 1.19 °C and decreased soil moisture (SM) by 0.02 m^3 m^{-3}, whereas the high-level warming increased T_s by 2.88 °C and decreased SM by 0.04 m^3 m^{-3} over the four growing seasons in 2014–2017. The low- and high-level increased precipitation did not affect T_s, but increased SM by 0.02 m^3 m^{-3} and 0.04 m^3 m^{-3}, respectively, over the four growing seasons in 2014–2017. No significant main and interactive effects of experimental warming and increased precipitation on R_s were observed over the four growing seasons in 2014–2017. In contrast, there was a significant inter-annual variation of R_s in 2014–2017. There was a marginally significant quadratic relationship between the effect of experimental warming on R_s and warming magnitude. There was a negligible difference of R_s between the low- and high-level increased precipitation over the four growing seasons in 2014–2017 and R_s also showed a quadratic relationship with precipitation. Therefore, experimental warming and increased precipitation did not change R_s and R_s responded nonlinearly to experimental warming and increased

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precipitation in the alpine meadow in the Northern Tibetan Plateau. Growing season precipitation may play a more important role than experimental warming and increased precipitation in affecting R_s in the alpine meadow in the Northern Tibetan Plateau.

1. Introduction

Soil respiration (R_s), as the second carbon flux in terrestrial ecosystems, is a main output pathway of soil organic carbon bank and an important source of atmospheric CO_2 (Raich and Potter, 1995). A very small change in R_s can have a strong impact on the global carbon balance (Cox et al., 2000; Li et al., 2018; Peng et al., 2015a; H. Wang et al., 2017). Response of R_s and its feedback to climatic change are important for the stability of ecosystem processes (Lu et al., 2013; Royer-Tardif et al., 2010). Therefore, accurately quantifying the response of R_s to climatic warming and its related mechanisms is of great importance for understanding global climatic change and predicting future change in atmospheric CO_2 concentration (Fang et al., 2017; Feng et al., 2017; Liang et al., 2004; Pries et al., 2017).

The magnitudes of climatic warming and increased precipitation vary with areas on the Tibetan Plateau (Diffenbaugh and Field, 2013; Kuang and Jiao, 2016). Several uncertainties remain, although many field warming experiments have been conducted to quantify the effect of experimental warming on R_s in the alpine meadow on the Tibetan Plateau (Ganjurjav et al., 2018; Lin et al., 2011; Peng et al., 2015a; Shi et al., 2012). First, most of these previous studies have only examined a single level experimental warming on R_s. Although the warming magnitudes may be different, the climatic conditions (e.g. mean annual temperature and precipitation) and vegetation conditions (e.g. community composition) can also be different among these previous warming experiments. Thus, it is hard to directly examine the relationship between the warming effect on R_s and warming magnitude using these previous warming experiments. These indicate that a multi-levels warming experiment is needed to better examine how R_s will respond to different warming magnitudes in the alpine meadow on the Tibetan Plateau. Second, only a few studies have compared responses of R_s to multi-levels experimental warming in the alpine meadow on the Tibetan Plateau, whereas there are no consistent reports on the relationship between warming magnitude and the response of R_s to warming (Peng et al., 2015b; Shen et al., 2016; Xiong et al., 2014). For example, Peng et al. (2015b) found that a low- and high-level experimental warming increased R_s by 18% and 29%, respectively. In contrast, Shen et al. (2016) demonstrated that a low- and high-level experimental warming did not significantly alter R_s. These indicate that more multi-levels warming experiments are needed. Only one study has compared effects of multi-levels increased precipitation on R_s in the alpine meadow in the Northern Tibetan Plateau (Shen et al., 2015). Moreover, no studies have examined the response of R_s to multi-levels warming and increased precipitation under controlled warming and increased precipitation conditions in the alpine meadow on the Tibetan Plateau. Therefore, it remains unclear how R_s will respond to multi-levels warming and increased precipitation in the alpine meadow on the Tibetan Plateau. More field multi-levels warming and increased precipitation experiments are needed.

In this study, a field multi-level warming (no, low- and high-level) and increased precipitation (no, low- and high-level) experiment was conducted in an alpine meadow in the Northern Tibetan Plateau. The main objective of this study was to examine the response of R_s to the multi-levels experimental warming and increased precipitation. We hypothesized that experimental warming and increased precipitation had nonlinear effects on R_s.

2. Materials and methods

2.1. Study area and experimental design

Our previous studies have made detailed descriptions on the characteristics of climate, soil and vegetation, and experimental design (Fu and Shen, 2017; Fu et al., 2018). Therefore, only a brief description was made in this study. Two heights (40 cm and 80 cm) of open top chambers (OTC) and two diameters (44 cm and 62 cm) of precipitation collection funnels were used to obtain two warming magnitudes and two increased precipitation magnitudes (15% and 30%), respectively, since early June 2014. The no warming and no extra precipitation treatment was labeled by 'C'. The OTCs with heights of 40 cm and 80 cm were the low- and high-level experimental warming treatments, and labeled by 'LW' and 'HW', respectively. The 15% and 30% increased precipitation treatments were labeled by 'LP' and 'HP', respectively. The 'LW + LP', 'HW + LP', 'LW + HP' and 'HW + HP' referred to the interactive effects between 'LW' and 'LP' treatments, between 'HW' and 'LP' treatments, between 'LW' and 'HP' treatments, and between 'HW' and 'HP' treatments, respectively.

2.2. Microclimate measurements and AGB estimation

During the whole study period (June–September in 2014–2017), soil temperature (T_s, 5 cm) and soil moisture (SM, 10 cm) was measured using HOBO micro-climatic stations (Onset Computer, Bourne, MA, USA). Aboveground biomass (AGB) was estimated by measured normalized difference vegetation index (NDVI) (AGB = $10.33e^{3.28NDVI}$) (Fu et al., 2013). These NDVI data were obtained using a Tetracam Agricultural Digital Camera (Tetracam Inc., Chatsworth, CA, USA) during the whole study period.

2.3. R_s measurement

We measured R_s using a CO_2 flux system (LI-8100, LI-COR Biosciences, Lincoln, NE, USA) during the period from June to September in 2014–2017. A daytime cycle of R_s (8:00 to 18:00 with a 2 h interval) was measured every month. A polyvinyl chloride (PVC) collar (diameter, 20 cm; height, 5 cm) was inserted 2–3 cm into the soil in the center of each plot in June 2014 and left the same place during the whole study period.

2.4. Statistical analyses

We used the SPSS 16.0 for data analysis. Responses of T_s, SM, AGB and R_s to warming, increased precipitation and measuring year were examined by repeated-measures analysis of variance. The differences of T_s, SM, AGB and R_s among no, low- and high-level experimental warming or among no, low- and high-level increased precipitation were examined by Duncan multiple comparisons. The exponential relationships between R_s and T_s, and linear relationships between R_s and SM were examined. The relationships between R_s and T_s and SM were examined by multiple linear regressions. Similar with our previous study (Fu et al., 2018), we calculated the response ratio of R_s to experimental warming (R_{w_Rs}) and increased precipitation (R_{IP_Rs}) in this study. The quadratic relationships between the logarithm of R_{w_Rs} and experimental warming-induced the increase in T_s (ΔT_s), and between growing season mean R_s and growing

Table 1
Multiple linear regressions between soil respiration (R_s), and soil temperature (T_s) and soil moisture (SM), showing changes in the regression coefficient, significance probability (p), coefficient of determination (R^2) and partial correlation coefficient. Natural logarithm transformations were made for R_s and SM before regression analysis.

Treatment		Coefficient	R^2	Partial correlation	p
C	Constant	1.20			<0.001
	T_s	0.07	0.19	0.50	<0.001
	SM	0.76	0.21	0.58	<0.001
LW	Constant	1.17			<0.001
	T_s	0.06	0.13	0.42	<0.001
	SM	0.65	0.28	0.61	<0.001
HW	Constant	1.82			<0.001
	T_s	0.03	0.05	0.31	0.002
	SM	0.76	0.54	0.76	<0.001
LP	Constant	1.16			<0.001
	T_s	0.06	0.12	0.40	<0.001
	SM	0.77	0.22	0.54	<0.001
LW + LP	Constant	0.84			0.001
	T_s	0.07	0.21	0.54	<0.001
	SM	0.73	0.27	0.66	<0.001
HW + LP	Constant	1.27			<0.001
	T_s	0.04	0.09	0.33	<0.001
	SM	0.59	0.21	0.54	<0.001
HP	Constant	0.46			0.064
	T_s	0.08	0.24	0.58	<0.001
	SM	0.57	0.28	0.61	<0.001
LW + HP	Constant	0.76			0.018
	T_s	0.08	0.18	0.49	<0.001
	SM	0.76	0.24	0.59	<0.001
HW + HP	Constant	2.30			<0.001
	T_s	−0.04	0.05	−0.24	0.018
	SM	0.39	0.19	0.39	<0.001

season precipitation (GSP) were examined. We also examined the linear relationships between R_{w_Rs} and GSP, R_{w_Rs} and growing season mean air temperature (GST), R_{w_Rs} and the response ratio of AGB to experimental warming (R_{w_AGB}), and R_{IP_Rs} and the response ratio of AGB to increased precipitation (R_{IP_AGB}).

3. Results

3.1. Variations of air temperature and precipitation

There were significant seasonal and inter-annual variations of air temperature (T_a) and precipitation (Fig. S1). The minimum monthly average T_a occurred in September 2014–2016, but in June 2017. The maximum monthly average T_a occurred in June 2014–2015, but in July 2016–2017. The minimum monthly total precipitation occurred in September 2014, 2015, and 2017, but in August 2016. The maximum monthly total precipitation occurred in August 2014–2015, but in July 2016–2017. The GSP in 2014 (437.30 mm) was the highest, and that in 2015 (300.20 mm) was the lowest among the four years. The GST in 2016 (10.52 °C) was the lowest, and that in 2017 (11.38 °C) was the highest among the four years.

3.2. Response of R_s to experimental warming and increased precipitation

No significant main and interactive effects of experimental warming and increased precipitation on R_s were observed (Table S1). There were also no significant differences of the temperature sensitivity of R_s among the 'C', 'LP' and 'HP' treatments. Regardless of increased precipitation, the low- and high-level experimental warming did not
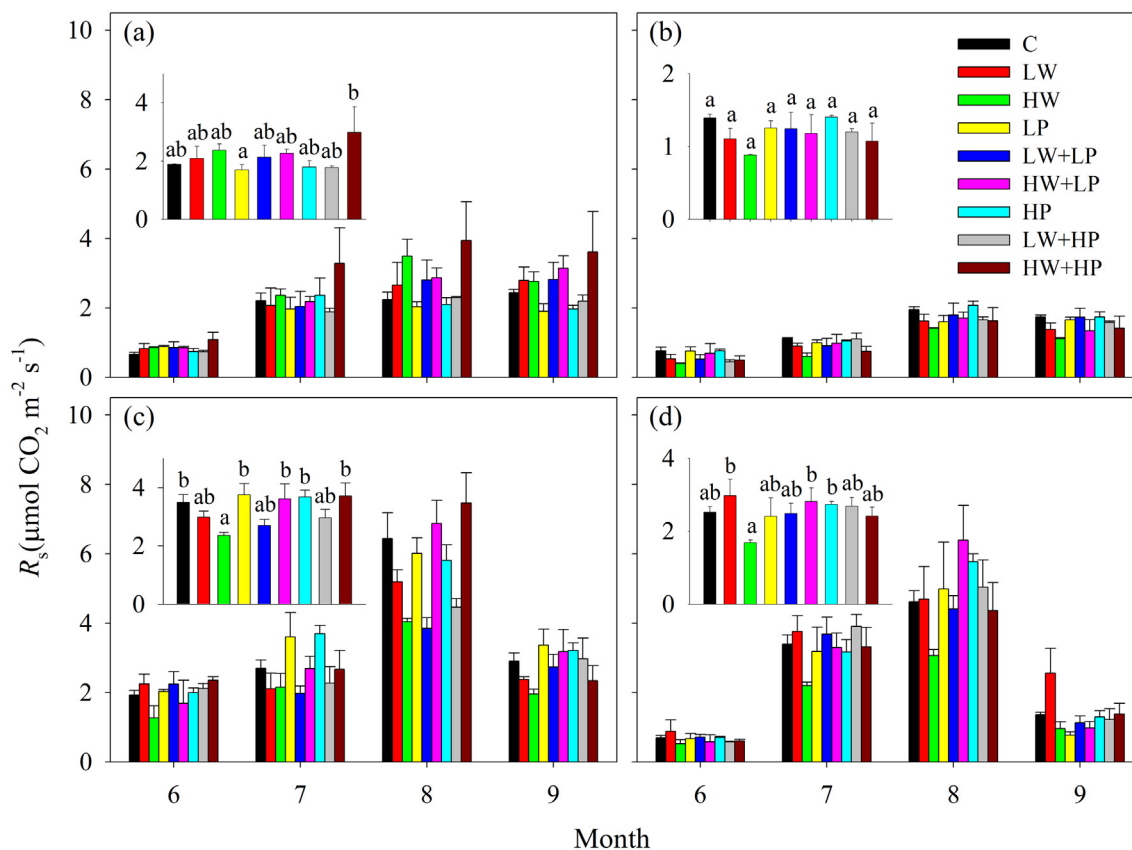
Fig. 1. Comparison of soil respiration (R_s) in (a) 2014, (b) 2015, (c) 2016 and (d) 2017 under different experimental warming and increased precipitation treatments. The inset plot in each subfigure was the average data during the growing season. Different letters in inset plots indicated there were significant differences at $p < 0.05$.
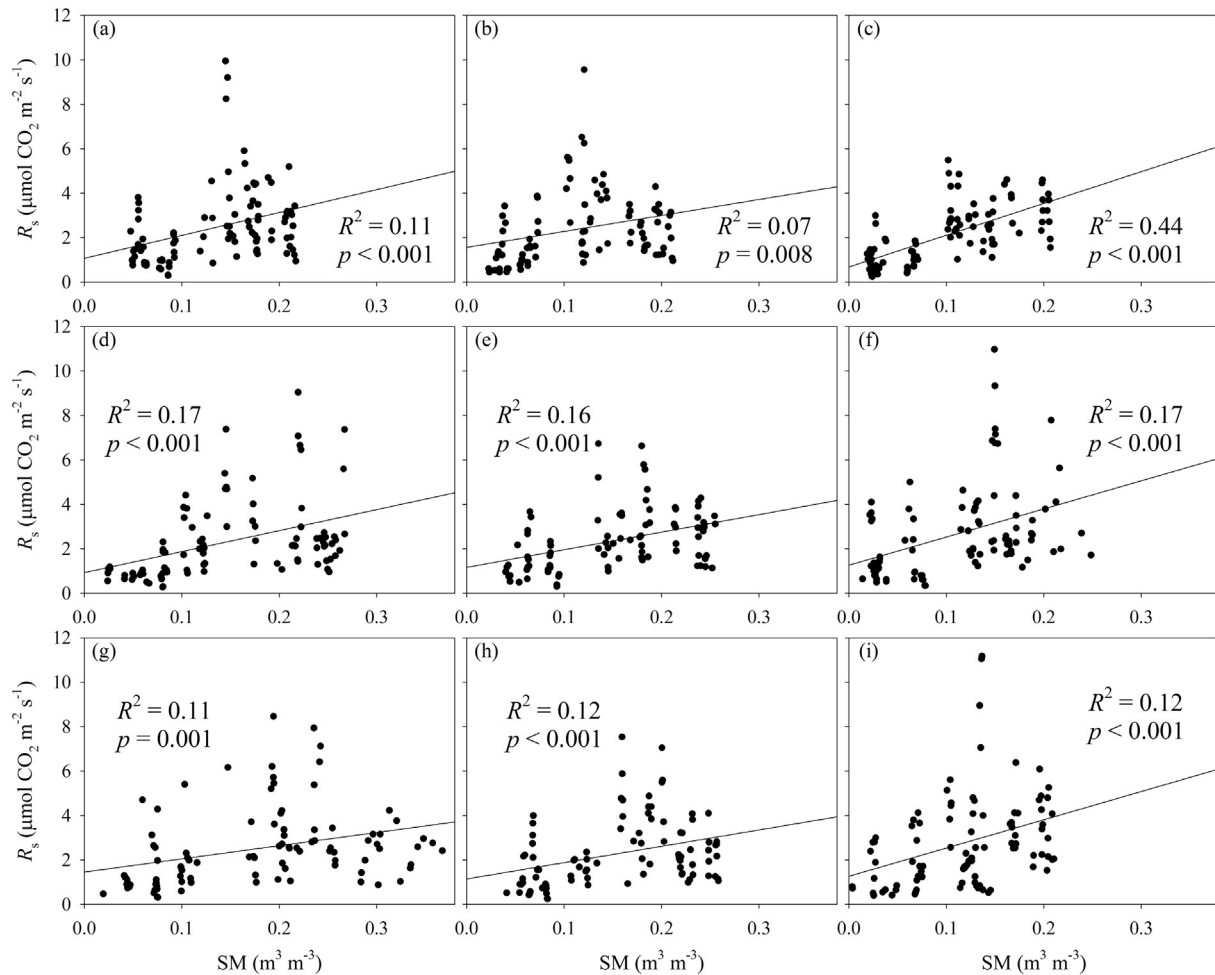
Fig. 2. Relationship between soil respiration (R_s) and soil moisture (SM) in the (a) control, (b) low-level experimental warming (LW), (c) high-level experimental warming (HW), (d) low-level increased precipitation (LP), (e) LW + LP, (f) HW + LP, (g) high-level increased precipitation (HP), (h) LW + HP and (i) HW + HP treatment.

significantly affect R_s, and there was a no significant R_s difference between the low- and high-level experimental warming across the four growing seasons. Regardless of experimental warming, the low- and high-level increased precipitation did not significantly affect R_s, and there was a no significant R_s difference between the low- and high-level increased precipitation across the four growing seasons. There was a significant interannual variation of R_s (Table 1, Fig. 1).

Effect of experimental warming on R_s varied with years (Table S1). Regardless of increased precipitation, the low-level experimental warming significantly decreased R_s in 2016 by 20.88% (0.76 μmol CO_2 m^{-2} s^{-1}). Regardless of increased precipitation, the high-level experimental warming significantly increased R_s in 2014 by 41.59% (0.75 μmol CO_2 m^{-2} s^{-1}), and significantly reduced R_s in 2015 by 22.61% (0.31 μmol CO_2 m^{-2} s^{-1}).

The R_s of the 'HW + HP' treatment was 75.71% (1.28 μmol CO_2 m^{-2} s^{-1}) greater than that of the 'LP' treatment in 2014 (Fig. 1). The R_s of the 'C', 'LP', 'HW + LP', 'HP' and 'HW + HP' treatment was 48.22% (1.14 μmol CO_2 m^{-2} s^{-1}), 59.16% (1.39 μmol CO_2 m^{-2} s^{-1}), 53.05% (1.25 μmol CO_2 m^{-2} s^{-1}), 56.11% (1.32 μmol CO_2 m^{-2} s^{-1}) and 57.39% (1.35 μmol CO_2 m^{-2} s^{-1}) greater than that of the 'HW' treatment in 2016, respectively (Fig. 1). The R_s of the 'LW', 'HW + LP' and 'HP' treatment was 76.49% (1.29 μmol CO_2 m^{-2} s^{-1}), 66.82% (1.13 μmol CO_2 m^{-2} s^{-1}) and 62.37% (1.05 μmol CO_2 m^{-2} s^{-1}) greater than that of 'HW' treatment in 2017, respectively (Fig. 1).

3.3. Response of T_s, SM and AGB to experimental warming and increased precipitation

There was a significant main effect of experimental warming on T_s and SM, respectively (Table S1). Regardless of increased precipitation, the low-level warming significantly increased T_s by 1.19 °C and significantly decreased SM by 0.02 m^3 m^{-3}, whereas the high-level warming significantly increased T_s by 2.88 °C and significantly decreased SM by 0.04 m^3 m^{-3} across the four growing seasons. There were no significant differences of T_s among the 'C', 'LP' and 'HP' treatments, the 'LW', 'LW + LP' and 'LW + HP' treatments, and the 'HW', 'HW + LP' and 'HW + HP' treatments across the four growing seasons, respectively (Fig. S2). The T_s was the largest for the 'HW', 'HW + LP' and 'HW + HP' treatments, the second largest for the 'LW', 'LW + LP' and 'LW + HP' treatments, and the smallest for the 'C', 'LP' and 'HP' treatments (Fig. S2). Experimental warming-induced the decline in SM significantly decreased with increasing experimental warming-induced the increase in T_s (Fig. S3). There was a significant main effect of increased precipitation on SM (Table S1). Regardless of experimental warming, the low-level increased precipitation significantly increased SM by 0.02 m^3 m^{-3} and the high-level increased precipitation significantly increased SM by 0.04 m^3 m^{-3} across the four growing seasons. Compared to the 'C' treatment, the 'HW' and 'HW + LP' treatment significantly reduced SM by 0.04 and 0.03 m^3 m^{-3}, and the 'LP' and 'HP' treatment significantly increased SM by 0.02 and 0.04 m^3 m^{-3} across the four
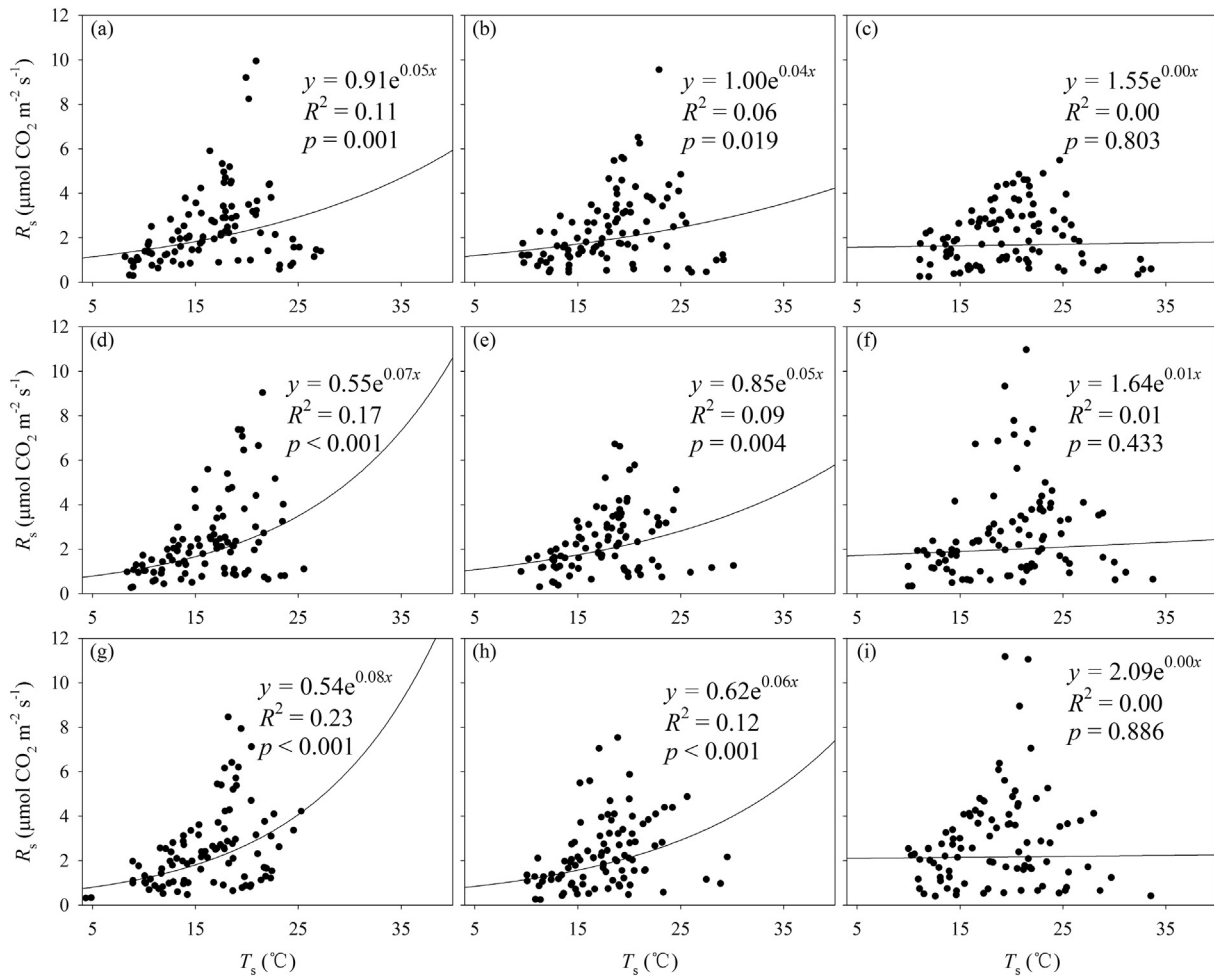
Fig. 3. Relationship between soil respiration (R_s) and soil temperature (T_s) in the (a) control, (b) low-level experimental warming (LW), (c) high-level experimental warming (HW), (d) low-level increased precipitation (LP), (e) LW + LP, (f) HW + LP, (g) high-level increased precipitation (HP), (h) LW + HP and (i) HW + HP treatment.

growing seasons, respectively (Fig. S2). Increased precipitation-induced the increase in GSP showed a significant positive relationship with increased precipitation-induced the increase in SM, but a marginally significant relationship with increased precipitation-induced the decline in T_s (Fig. S4).

There was a significant main effect of increased precipitation on AGB (Table S1). Regardless of experimental warming, the high-level increased precipitation significantly increased AGB by 12.83% (2.29 g m^{-2}) across the four growing seasons. The AGB of 'LW + HP' treatment was 22.32% (3.80 g m^{-2}) greater than that of 'C' treatment across the four growing seasons (Fig. S2). However, there was a no significant main effect of experimental warming on AGB (Table S1). Regardless of increased precipitation, there was also a no significant AGB difference between the low- and high-level experimental warming across the four growing seasons.

3.4. Relationships between R_s and microclimates, and AGB

The R_s significantly increased with increasing SM for all the nine treatments, and increased with increasing T_s only for the 'C', 'LW', 'LP', 'LW + LP', 'HP' and 'LW + HP' treatments (Figs. 2, 3). The T_s and SM together explained the variation of R_s, and SM explained more variation of R_s compared to T_s for all the nine treatments (Table 1). The logarithm of R_{w_Rs} showed a marginally significant quadratic relationship with experimental warming-induced the increase in T_s (Fig. 4). The R_{w_Rs} significantly increased with increasing growing season precipitation (GSP)

(Fig. 5). The R_s showed a significant quadratic relationship with GSP (Fig. 6). The R_{w_Rs} significantly increased with increasing R_{w_AGB}, and R_{IP_Rs} was not significantly correlated with R_{IP_AGB} (Fig. 7).
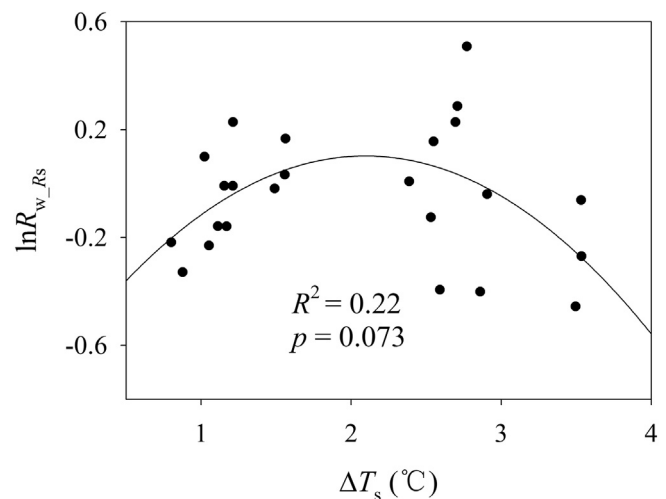
Fig. 4. Relationship between the logarithm of response ratio of soil respiration to experimental warming ($\ln R_{w\_Rs}$) and increased magnitude of soil temperature (ΔT_s).
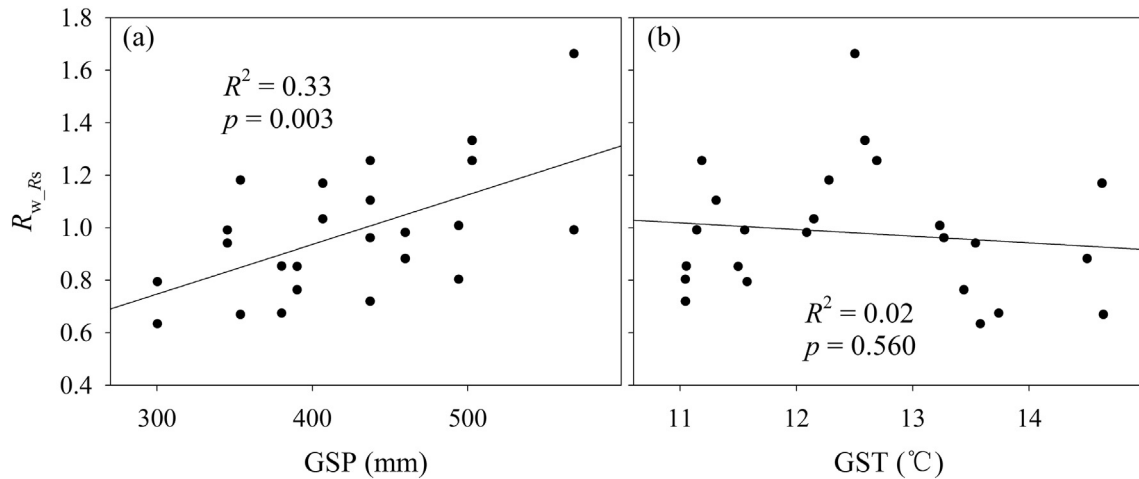
Fig. 5. Relationship (a) between the response ratio of soil respiration to experimental warming (R_{w_Rs}) and growing season precipitation (GSP); and (b) between R_{w_Rs} and growing season temperature (GST).

4. Discussion

4.1. Effects of warming

Our findings suggested that R_s was more sensitive to experimental warming in wetter environments. This phenomenon was in similar with several previous studies which demonstrated that water availability can regulate the response of R_s to experimental warming in alpine grasslands (Peng et al., 2015a; Shen et al., 2015). Our findings indicated that climatic warming may not always increase R_s, which was in line with some previous studies conducted on the Tibetan Plateau (Chen et al., 2016; Shen et al., 2016).

Our findings were in consistent with several previous studies which indicated that no significant main effects of experimental warming on R_s were observed (Briones et al., 2009; Wan et al., 2007). One or more of the following mechanisms could explain this phenomenon. First, experimental warming can result in not only direct and positive effect on T_s but also indirect and negative effect on SM (Fu et al., 2018; Shi et al., 2012). Soil drying can dampen the positive effect of T_s on R_s (Shen et al., 2015; Zhong et al., 2016). Second, experimental warming-induced warming magnitude may deviate from the optimum warming magnitude for R_s (2.10 °C).

Our findings were in line with several previous studies which demonstrated that there was a no significant difference of R_s between low- and high-level experimental warming treatments (Shen et al.,

2016; Zhong et al., 2016). This phenomenon could be explained by one or more of the following reasons. First, although the increased magnitude of T_s under the high-level experimental warming (2.88 °C) was closer to the optimum warming magnitude for R_s (2.10 °C) than that under the low-level experimental warming (1.19 °C), the low-level experimental warming caused a lower soil drying. Second, the temperature acclimation of R_s increased with increasing warming magnitude (Suseela and Dukes, 2013; Wang et al., 2014). Third, our previous study (Fu et al., 2018) indicated that there was a negligible difference of AGB between the low- and high-level experimental warming. This study implied that R_s and AGB may have synergy changes under controlled experimental warming conditions. Thus, the no significant difference of R_s between the low- and high-level experimental warming can be also related to that of AGB (Shen et al., 2016; J.W. Wang et al., 2017).

4.2. Effects of increased precipitation

Our findings implied that increased precipitation may not always increase R_s and R_s responded nonlinearly to increased precipitation. This phenomenon can be explained by one or more of the following reasons. First, increased precipitation-induced the increase in SM can have a positive effect on R_s, which may be dampened by increased precipitation-induced the decline in T_s (Lellei-Kovács et al., 2008; Munson et al., 2010; Zhou et al., 2006). Moreover, a greater increase in precipitation can result in a greater decline in T_s (Shen et al., 2015). Second, increased precipitation can also have a nonlinear impact on the temperature sensitivity of R_s (Shen et al., 2015).

Our previous study (Fu et al., 2018) and this study indicated that the high-level increased precipitation significantly increased gross primary production and AGB rather than R_s. These results implied that the high-level increased precipitation may lead to net carbon gains in the alpine meadow of the Northern Tibetan Plateau. Precipitation is predicted to continue to increase in the 21 century on the Tibetan Plateau (Ji and Kang, 2013), which in turn may result in net carbon gains in alpine grasslands in the Northern Tibetan Plateau.

4.3. Interactive effects of warming and increased precipitation

Our findings were in line with several previous studies (Liu et al., 2009; Wan et al., 2007; Zhou et al., 2006) which found that there was lack of a significant interactive effect of experimental warming and increased precipitation on R_s. Our previous studies demonstrated that there were no significant interactive effects of experimental warming and increased precipitation on plant production and R_s was positively
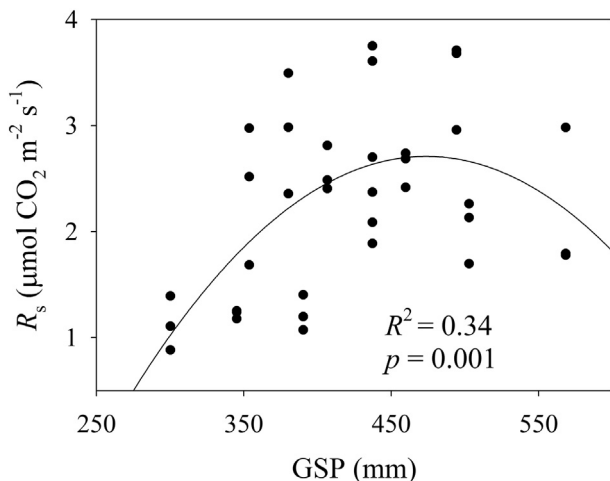
Fig. 6. Relationship between soil respiration (R_s) and growing season precipitation (GSP).
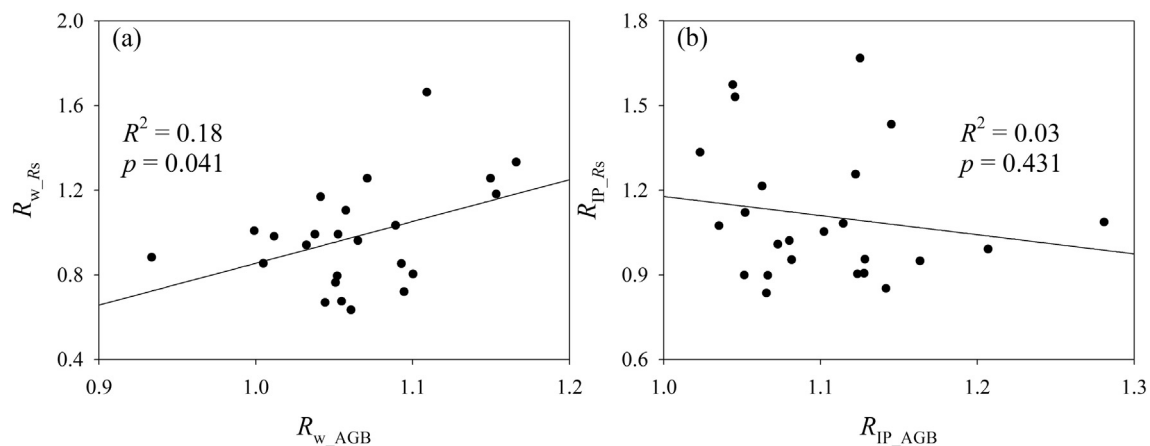
Fig. 7. Relationship (a) between the response ratio of soil respiration (R_s) to experimental warming (R_{w_Rs}) and the response ratio of aboveground biomass (AGB) to experimental warming (R_{w_AGB}); and (b) between the response ratio of R_s to increased precipitation (R_{IP_Rs}) and the response ratio of AGB to increased precipitation (R_{IP_AGB}).

correlated with AGB (Fu et al., 2018; Fu et al., 2014). Therefore, the negligible interactive effect of experimental warming and increased precipitation on R_s across the four growing seasons in 2014–2017 can be linked to that of plant production.

4.4. Interannual variation of precipitation had a stronger effect on R_s than did experimental warming and increased precipitation

Our results was similar with several previous studies which found that the interannual variation of R_s was stronger than the effect of experimental warming on R_s (Chen et al., 2016; Peng et al., 2014; Shen et al., 2016). This phenomenon can be explained by one or more of the following reasons. First, the negligible response of R_s to experimental warming may be due to experimental warming-induced soil drying and warming magnitude deviated from the optimum value mentioned above. Second, the maximum GSP difference (137.1 mm) among years under the natural precipitation conditions in 2014–2017 was greater than the increased magnitude of GSP (45.0–131.2 mm) under increased precipitation conditions. Moreover, precipitation rather than temperature can predominate the variation of R_s (Chen et al., 2016; Xia et al., 2009; Zhou et al., 2007). Thus, the significant interannual variation of R_s can be related to the high GSP difference among years.

5. Conclusions

There were no significant main and interactive effects of experimental warming and increased precipitation on R_s. Both climatic warming and increased precipitation can have nonlinear effects on R_s in the alpine meadow. Therefore, we may manage the alpine meadow by classification under climatic change conditions considering that the magnitudes of warming and precipitation change can vary with regions in the alpine meadow on the Tibetan Plateau. However, there are other various alpine grasslands (e.g. the alpine steppe) on the Tibetan Plateau, besides the alpine meadow. Therefore, to better understand the nonlinear response of alpine grasslands to climatic change, more field multi-levels warming and increased precipitation experiment are needed.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2018.08.111.

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